

# IMPROVEMENT AND GENETICS OF TOMATOES, PEPPERS, AND EGGPLANT

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## TOMATO

IN SO FAR as we are able to tell from written record, the tomato is a very new crop (18).<sup>1</sup> The oldest records of it date back less than 400 years, a brief time when compared with the oldest available records of many other crops. The tomato is of tropical American origin, and early reports indicate that it was planted in maize fields and eaten by the ancient Mexicans, who called it *tomati*. Apparently it attained no very important place in the lives of those people, perhaps on account of the highly perishable nature of the edible fruit and the absence of known means for its preservation. Although it is believed to be native to the same regions as certain early forms of maize, there are no known prehistoric remains, no prehistoric sculpture or ceramics to record its early culture as in the case of maize, kidney beans, lima beans, and squash in North America, or wheat and numerous other plants in the East. We thus are able to form no definite idea of its antiquity and early importance. The absence of record or remains of plant parts might imply relative unimportance and little use. On the other hand, the earliest references in the literature describe essentially the same forms that are grown today. No new markedly different fruit types are known to have appeared since, and the large forms have never been found truly wild. It is therefore believed that the tomato was already improved far beyond the wild state when North America was discovered. Even so, our smooth, large, symmetrical-fruited varieties of today are in marked contrast to the rough, variable types known in this country a century ago.

We have all heard how the able, up-and-coming young man is rarely appreciated in his native environment but must go abroad to make good, and then returns to receive the approval of his countrymen. Some of our native American crops, including the tomato, have gone through a similar experience. The potato, native to the New World, is called "Irish potato" because colonial America repatriated it to the New World from Ireland, where it had become a very important crop while it was being ignored close to its native land. The tomato was introduced into Europe early in the sixteenth century and became widely distributed. In the seventeenth century it was grown in England for ornament only, although it was known to be eaten elsewhere. By the end of the eighteenth century it was grown

<sup>1</sup> Italic numbers in parentheses refer to Literature Cited, p. 204.

on a field scale in Italy and used extensively as food, but it was a half century more before people in the United States generally dared to eat it.

#### EARLY VARIETAL ADAPTATION

Although each of several countries in which tomatoes are grown to any large extent usually has a number of varieties that show a considerable range in varietal characteristics among themselves, the group of varieties grown in each region is rather distinct from those grown in certain other parts of the world. Not every country has its own distinct general type, but there are marked differences between geographic areas. It is probable that definite selection and breeding work with the tomato for adapting it to warm-temperate and cool-temperate regions has been in progress but a short time, not over two centuries and perhaps only half that. Nevertheless, in a certainly brief span this tropical or subtropical plant has been adapted to a wide range of environments far different from its native home. The efforts at selection by early growers of the crop together with natural factors produced a very interesting and effective assortment of general types, each of which apparently points toward the maximum adaptability in each region.

The best Italian varieties in general are of long season and are large, vigorous growers, with a profusion of thick-walled fruits of unusually brilliant color and high content of solids. A wide range in fruit size exists among these varieties, some of the most valuable being small, as judged by United States preferences. The important point is that those varieties do better in Italy than elsewhere and are better for Italian purposes than others that have been tried in Italy.

There is a considerable outdoor culture of tomatoes in Germany and some adjacent north-European areas. The varieties grown there are early, relatively small-vined, and medium- to small-fruited.

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*THE early tomato breeders did excellent work in producing plants with good yields of large handsome fruits, adapted to local or regional conditions; but the situation has changed, and new problems and requirements have arisen so fast that it is not now possible to keep ahead of them by the old method of selecting chance variants in the field. Systematic effort is necessary to find and bring together characteristics that will make entirely new varieties resistant to specific diseases and to heat and cold, and adaptable to long-distance shipment, to new areas of culture, to new processes or means of utilization. This is the kind of work being done by State and Federal agencies. The disease problem especially is so important today that practically no research agency would introduce any new variety unless it were resistant to at least one very troublesome disease.*

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Italian and most United States varieties are not adapted to the climate of Germany, and the German varieties when grown in the United States are distinctly inferior to our own. Except for color differences, the north-European sorts are largely of the one general type described.

As mentioned in the introductory article on vegetables, the English have developed a characteristic type of greenhouse tomato, some varieties of which are practically parthenocarpic, requiring no pollination, by hand or otherwise, as American varieties do, in order to set fruit. These varieties are very prolific, setting very large numbers of fruits that are too small to suit American growers and consumers—but they are well adapted to the region and to the purpose for which they are grown. They were the first improved varieties in the modern sense.

In a large country like the United States, with a climatic range from subtropical to cool temperate and from humid to arid, different variety groups have been developed to suit different parts of the country. Until about 10 years ago most of this adaptation had been effected by private growers and seedsmen, who selected chance variants or the progeny of natural crosses that were particularly promising in a given region. A few of the old important varieties were the results of artificial hybridizing. Extensive commercial tomato production in this country is not much over 50 years old. Sixty years ago the only large sorts were rough, ugly, heavily ribbed, variable “varieties” of indifferent quality, although some good small ones of the greenhouse type had been brought in from England.

The old varieties were certainly quite heterozygous or mixed in their hereditary composition, for the tomato frequently crosses naturally in the field. Bailey (3) and others have referred to tomato varieties running out. These cases were doubtless due to the effects of more or less accidental selection within very mixed populations. These few rough and ready mixtures, our early so-called varieties, were the confused mass of raw material from which so many of our really good varieties have been selected, directly or indirectly, by keen-eyed growers. Tomatoes are now grown commercially in every State in this country.

#### IMPROVEMENT IN THE UNITED STATES, 1850-1910 <sup>2</sup>

Prior to 1860 no tomato varieties had been developed in the United States. The few varieties known had been brought in chiefly from England and a few from France. It appears that most of the large-fruited varieties, if not all of them, had been obtained by selection from the old Large Red or ribbed type that had been known since about 1550. The smaller fruited, more prolific forcing or greenhouse types and similar sorts presumably were first selected from the round tomato (smooth), which was originally described by Tournefort about 1700. Since there has been only a minor interest in the small-fruited forms in this country, a chronology of tomato improvement will be confined largely to the story of the old Large Red and its descen-

<sup>2</sup>In the preparation of this historical review the writer has freely used unpublished notes and records in the files of the Division of Fruit and Vegetable Crops and Diseases made by the late W. W. Tracy, Sr., and by D. N. Shoemaker and other former staff members.

dants. The old Round, however, has apparently contributed some genes of value. The cherry-, pear-, and plum-shaped tomatoes have been known as long as the Large Red but have undergone no appreciable change.

Probably the first true dwarf or "tree" variety, named Tree, was introduced by Vilmorin-Andrieux & Cie., of Paris, in 1860, and was promptly brought into this country. It was found as a chance variant in a tall variety by a private gardener of an estate at Chateau de Laye in France. Two other imported varieties of interest in the United States, introduced about that time, were Fiji Island (1862) and Cook Favorite (1864). Several forcing types of European origin were being grown, but their origin is obscure.

Probably the first United States contribution to tomato improvement was the introduction of the Tilden variety by Henry Tilden, of Davenport, Iowa, in 1865. It originated as a chance seedling in a field of a variety the name of which is not recorded (3).

The next notable advance occurred in 1870 with the introduction of Trophy, a result of hybridization and selection by a Dr. Hand, of Baltimore County, Md. It is said to have been from a cross of Large Red  $\times$  Early Red Smooth. The variety was introduced by G. E. Waring, of Newport, R. I., who received it as a supposedly fairly well-fixed stock from T. J. Hand, the son of the originator. It has been stated that Trophy was involved in the parentage of most of the varieties introduced in the following quarter century, and undoubtedly it has contributed, at least indirectly, to a great number of later varieties. The old original Trophy was evidently not very well fixed, however, for

before 1900 it had practically ceased to exist (3). Through both purposeful and accidental hybridization, and through artificial selection and natural selection within a rather heterozygous variety, superior variants were saved and inferior ones discarded. There is evidence, too, that the perpetuation and increase of undesirable variants appearing in the variety (running out) as a result of segregation, natural crossing, mechanical mixture, or combinations of these, hastened the demise of the variety.

The work of A. W. Livingston (fig. 1), of Columbus, Ohio, and his associates and successors in the Livingston Seed Co. has resulted in the introduction of more new varieties than that of any other private group. Most of the varieties introduced by the Livingstons were of their own



Figure 1.—A. W. Livingston (1822-98), pioneer tomato breeder of Columbus, Ohio, who developed many tomato varieties still in current use.

finding or origination, but some were obtained from other growers. Paragon, from a chance seedling, was their first introduction (1870).

The famous old variety Acme was developed by A. W. Livingston from a single superior plant found in a field of mixed stock and introduced in 1875. Like the Trophy, this variety was the source or served as one parent of many subsequently introduced varieties. In 1880 Perfection, a chance variant in Acme, was introduced. Livingston next brought out Golden Queen in 1882, Favorite in 1883, Beauty in 1886, Potato Leaf in 1887, Stone (4) in 1889, and Royal Red in 1892. This last was developed from seven similar plants found in a field of Dwarf Champion by M. M. Miesse. The others just named were chance seedlings occurring in varieties the names of which are not known. These were followed by Aristocrat and Buckeye State in 1893, Honor Bright in 1897, and Magnus in 1900, as chance seedlings in varieties not recorded. In 1903 Dwarf Stone was introduced; it was a chance seedling found in Stone. Globe (4) is from a cross between Stone and Ponderosa made about 1899 by Robert Livingston and was introduced in 1905. Hummer, another introduction, was selected out of Paragon.

Of this impressive list introduced by the Livingstons, Stone and Globe are among the most important varieties grown today. Acme, Beauty, Buckeye State, Dwarf Stone, Golden Queen, and Perfection are still listed by some seed producers although they are not extensively grown.

In 1882 D. M. Ferry & Co. obtained a selection made by a farmer grower from an unknown variety, and they introduced it in 1885 as Optimus.

Some introductions of W. Atlee Burpee & Co. were Matchless, introduced in 1889; Fordhook Fancy, a production by E. C. Green, of the Ohio Agricultural Experiment Station, in 1898; Combination (Lorillard  $\times$  Acme  $\times$  Comet) in 1896; and Quarter Century in 1899—a cross between Lorillard and Dwarf Champion. These last two were developed by Walter Van Fleet, then of the Rural New Yorker.

In 1887, at the Michigan Agricultural College, L. H. Bailey selected a single outstanding plant from a plot of a German variety, Eiformig Dauer. This was released as the Ignotum variety and proved to be of major importance for many years.

Several varieties that had attained importance prior to 1910 are either of obscure parentage or their parentage has been reported and the introducer's name is not definitely known. Lorillard, named for its producer, was introduced in 1888 and was said to be from a cross between Acme and Perfection. The following are of unknown parentage: Chalk Early Jewel, by Moore & Simon in 1900; Ponderosa, by Peter Henderson in 1891; Early Detroit (4), from seed obtained from a Mr. Rosendahl, of Fort Leavenworth, Kans., introduced in 1909 by D. M. Ferry & Co.

The Stone variety has been the supposed parent stock of several varieties of considerable importance, among them Dwarf Stone, mentioned above; Earliana (4), found by George Sparks, of Salem, N. J., and introduced in 1900 by Johnson & Stokes; Greater Baltimore (4), found by John Baer, of Baltimore, Md., and introduced by J. Bolgiano & Sons in 1905.

Johnson & Stokes introduced Bonny Best (4) in 1908. It came from a single plant selection in a field of Chalk Early Jewel by G. W. Middleton, of Jeffersonville, Pa.

With all due credit to the important contributions of other growers seedsmen, and investigators, it is not out of place to call attention again to the great contribution of the Livingston Seed Co. to tomato improvement. Of about 40 varieties that had attained a distinct status prior to 1910, a third were productions of or introductions by the Livingston company. If we add those varieties derived directly from Livingston productions and introductions, it appears that half of the major varieties were due to the abilities of the Livingstons to evaluate and perpetuate superior material in the tomato.

#### PRIVATE INTRODUCTIONS, 1910-36

Due credit must be given the early workers mentioned in the preceding pages. Their object was to get good yields of large handsome fruits borne by plants adapted to local or regional conditions, and they succeeded admirably—so well, in fact, that about half of the 40 important varieties known in 1903 are still listed by at least a few of the larger producers and dealers. A few varieties, notably Chalk Early Jewel, Earliana, Ponderosa, Stone, and the dwarf sorts are universally listed. This older type of effort still continues, and from time to time some quite worth-while strains result from it. In comparison with the period 1875 to 1900, however, the old method of selection and crossing among present commercial sorts has in recent years resulted in a smaller number of marked improvements. Many of those obtained have been of value, particularly with respect to regional adaptation and suitability for long-distance shipping or for manufacture.

The Cooper Special, a variety with a distinctive, determinate, or "self-topping" habit of vine growth, was introduced by C. D. Cooper, a farmer near Fort Lauderdale, Fla. It was found as a chance seedling by Bert Croft in Florida in 1914.

Grand Rapids Forcing, long a popular greenhouse variety, was produced by John Nellist, a grower near Grand Rapids, Mich., by crossing Bonny Best and Comet, an English variety.

In 1915 John Baer, of Baltimore County, Md., turned over a selection from Bonny Best, which was named John Baer, to J. Bolgiano & Sons for introduction. Although similar to Bonny Best in many respects, this strain or variety seems particularly adapted to the north-eastern group of tomato-growing States and is often preferred to other stocks offered under the name of Bonny Best.

In 1920 the Everett B. Clark Seed Co. introduced an early shipping variety, named Clark Early, for culture mainly in the South. It was obtained by selection. D. M. Ferry & Co. in 1921 introduced Gulf State Market, a variety very similar to Globe but a trifle earlier in the South and less susceptible to cracking. It was found as a single plant in a field of Early Detroit by Walter Richards, of Crystal Springs, Miss., in 1917.

The J. T. D. is an interesting example of a local type developed for adaptation to a specific set of conditions and needs. It was developed

by the Campbell Soup Co. for growing in New Jersey, mainly for its own factory use. It has not become widely grown elsewhere.

In addition to these rather distinct sorts, several commercial firms and seed growers have given special attention to the isolation of superior stocks and strains of a number of the leading commercial varieties. Some of these stocks have been introduced under new names but frequently with only slight variation in the accepted name. A new name or a modified name does not, of course, insure improvement or even a difference. It may fairly be stated, however, that a number of these carefully handled "special" commercial strains of well-established varieties have proved to be superior to stocks generally available under the common name.

#### IMPROVEMENT BY PUBLIC AGENCIES

A discussion of the research that makes possible more rapid and orderly improvement of the tomato will be found in the section on Studies of Inheritance and Cytology at the end of this article. At this point will be presented a historical review of the new varieties introduced by State agricultural experiment stations and the United States Department of Agriculture.

In the last 25 years new problems and requirements have arisen so fast that tomato breeders cannot find naturally occurring chance variants with the desired characteristics fast enough to keep ahead of requirements. Special efforts are necessary to find and bring together these newly required features to produce new combinations, entirely new and different varieties. Of course the old objectives of large, smooth, high-quality fruit and high yields are still sought, but they must be in combination with such factors as tolerance or resistance to specific diseases, to heat, to cold, and adaptability to long-distance shipment, to new areas of culture, and to new processes or means of utilization. These characteristics are difficult to find and combine quickly with other desired properties.

Introductions prior to 1910 by public agencies were few and far between. Reference has already been made to *Ignotum*, selected by Bailey at the Michigan Agricultural College, and *Fordhook Fancy*, produced by Green at the Ohio station.

The major part of the tomato breeding by State and Federal agencies has been done in efforts to develop varieties resistant to disease. Thus far most attention has been devoted to resistance to fusarium wilt (fig. 2), but resistance to other diseases has also been sought, namely, nailhead rust, leaf spot, leaf mold, mosaic, and curly top. The disease problem in general has become so important that today there is little inclination on the part of research agencies to introduce any new tomato variety unless it is resistant to at least one very troublesome disease.

Selection for resistance to fusarium wilt was first started in 1910 by Essary (15), of the Tennessee Agricultural Experiment Station, and by Edgerton (13), of the Louisiana station. Two years later Essary distributed a resistant strain of the general type of *Beauty* but with a scarlet fruit like the color of *Stone*. This new sort, developed by mass selection from a diseased field near Gibson, Tenn., became known as

Tennessee Red. Later Essary distributed a wilt-resistant variety with scarlet-red fruit, named Tennessee Pink, also developed by mass selection in seriously diseased fields. Edgerton, in Louisiana, announced his first wilt-resistant sort in 1912. It was called Louisiana Wilt Resistant and was developed from a single resistant plant selected in a badly infected field of Aeme.

Although Louisiana Wilt Resistant proved highly resistant to the disease, it was late and a poor yielder. Edgerton crossed it in 1912 with the Langdon strain of Earliana to get earliness and fruitfulness. From the progeny of this hybrid a scarlet and a scarlet-red strain—

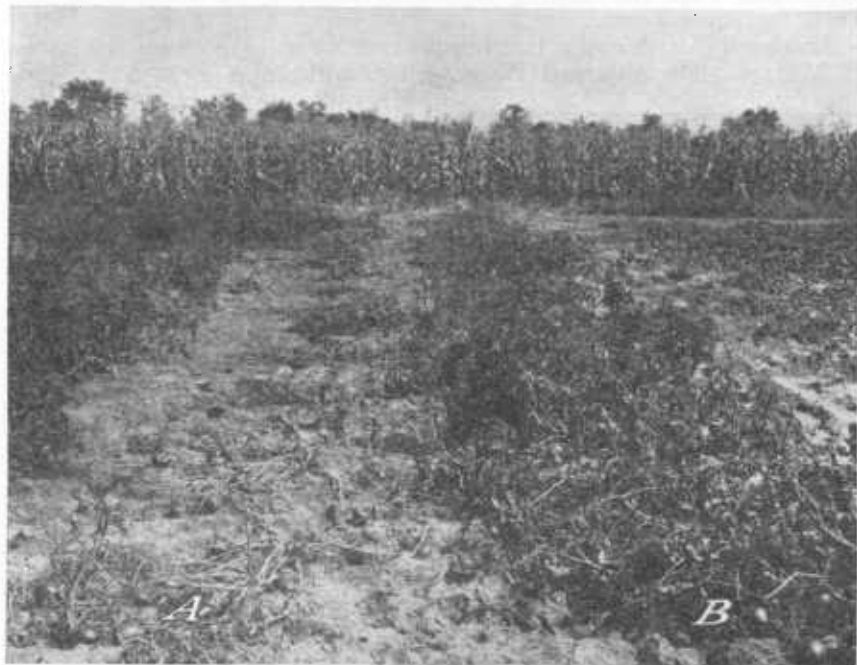


Figure 2.—A comparison of wilt-susceptible (A) and wilt-resistant (B) varieties of tomatoes on heavily infected land.

commonly called “red” and “pink”, respectively—were isolated, named Louisiana Red and Louisiana Pink, and distributed about 1918.

Norton (40), of the Maryland station, began selection for wilt resistance in 1912, selecting from a large number of varieties grown near Preston, Md., on a field naturally heavily infected. A number of unnamed resistant selections were distributed in 1915 to tomato growers and investigators. One of these, a wilt-resistant strain of Greater Baltimore, was further selected and grown for seed for several years by O. W. Twilley, of Hurlock, Md. In 1912 Norton selected a wilt-resistant sort from a field of badly damaged mixed varieties near Vienna, Md. This was included among strains given in 1915 to F. J. Pritchard (fig. 3), of the Department of Agriculture, who started his disease-resistant improvement work in that year. Two years of fur-



ther selection in this strain by Pritchard resulted in the Norton variety, distributed in 1917 by the Department and named for the man who made the original resistant plant selection. Two other resistant strains that Norton gave to Pritchard in 1915 were selected by the former from fields of Greater Baltimore. Pritchard selected them further under conditions of heavily artificially infected soil and distributed them in 1918 under the names of Columbia and Arlington. These three varieties, Norton, Columbia, and Arlington (42), developed by the informal joint efforts of the Maryland Agricultural Experiment Station and Department workers, were widely disseminated and were the leading resistant varieties, particularly in the East, for some years.

Pritchard distributed a third improvement in 1918 under the name of Marvel. He obtained it by selection from a French variety, Merveille des Marchés (Marvel of the Market), which shows a rather high and fairly uniform resistance (42).



Figure 3.—F. J. Pritchard, of the United States Department of Agriculture, who did notable work in breeding improved disease-resistant varieties of tomatoes.

Since 1917 the wilt-resistant varieties produced by the Department have greatly predominated over those originated by others. For reasons not entirely clear, those produced by various State experiment stations have remained more or less localized, and the total acreages of them are not very great. It may be that in the course of production and testing the limited opportunities of determining wide adaptability resulted in selections that were especially adapted to a rather narrow range of conditions; or it may be that the larger resources of the Department made possible not only more extensive tests but larger supplies of seed for original distribution and more effective dissemination of information about the new sorts. It seems

probable that some of the State work has resulted in varieties quite the equal of the Department sorts now commonly grown, or even superior to them in some respects, but still the latter dominate the field.

It should be recognized here that some of the first stocks of certain Department varieties distributed were the result of massing a number of selections that were apparently similar under the conditions of selecting. Under other growth conditions, undesirable variations in fruit and plant form appeared. Numerous State and private agencies have contributed to the success of these varieties by careful roguing or selection within the early stocks, keeping them in closer conformity to the ideals for the respective sorts.

In 1922 Pritchard introduced Norduke, a cross (Norton  $\times$  Duke of York) between two resistant sorts. Marvana (Marvel  $\times$  Earliana) and Marvelosa (Marvel  $\times$  Ponderosa) followed in 1924. All these earlier introductions by the Department are still listed by commercial firms (most firms list only one or a few of them), but they are unimportant and are not generally grown except in certain localities. Subsequent superior productions have largely displaced them.

The Marglobe (4), introduced by Pritchard and Porte in 1925, is without doubt the most important variety of tomato in the United States and in the world today. Its range of adaptability to both environmental and utilitarian requirements and its dominant position have been surprising. Marglobe is the result of a cross between Globe and Marvel made in a greenhouse of the Department in Washington in 1918. Globe has considerable resistance to wilt but is very susceptible to nailhead rust. Marvel is highly resistant to both. Marglobe proved highly resistant to wilt under most conditions and to nailhead under all conditions of which there is record. It was introduced just in time to save the Florida tomato-shipping industry from virtual extinction through the ravages of nailhead and wilt. It was developed primarily as a shipping tomato, but it has turned out to be the principal canning variety in the Middle Atlantic and South Atlantic States, as well as the leading shipping variety of the whole Atlantic region. It was the dominant variety in Mexico during the heyday of the tomato-shipping industry in that country; it is one of the best varieties recommended in Australia, and it is currently listed by commercial vegetable seedsmen in many foreign countries. The Marglobe has been to the present generation what Trophy and Acme were two generations ago. But ultimately, perhaps before long, it will be superseded by still better sorts, for, like all varieties, it has its limitations. It cracks rather badly, particularly in the Middle West, and it is not appreciably resistant to a number of diseases that are becoming increasingly important.

Three more recent productions by Pritchard and Porte should be mentioned before returning to some of the earlier work of the State stations. Marglobe was a parent in two of these—Break o' Day (Marglobe  $\times$  Marvana), introduced in 1931, and Pritchard<sup>3</sup> (Cooper Special  $\times$  Marglobe), introduced in 1932. Break o' Day was received much more enthusiastically than Pritchard, as a result of preliminary trials; but it has subsequently slipped into a relatively unimportant place, largely because it fails to meet rigid color requirements under most conditions. Pritchard, however, has become very popular on account of its superior scarlet color, despite the fact that it tends to bear most of its crop in a short time. It was expected to be of no value to canners because of this habit, but it is being used more each year. The third variety, Glovel<sup>4</sup> (Globe  $\times$  Marvel), is a "sister" to Marglobe but is scarlet-red ("pink") instead of scarlet ("red"). It is otherwise rather similar to Marglobe and is especially interesting because it cracks much less than Marglobe. Although reports on it

<sup>3</sup> Introduced under the name of Scarlet Topper. Renamed Pritchard in 1932 after Pritchard's death in January 1931.

<sup>4</sup> Produced in cooperation with the Florida Agricultural Experiment Station.

are generally good, it is too early to determine its value, since it was introduced in the spring of 1935 and first grown commercially in 1936. These last three varieties are all resistant to both fusarium wilt and nailhead.

The most important variety in the middle-western canning area of Illinois and Indiana is the Indiana Baltimore, developed by the Indiana Agricultural Experiment Station by selection from Greater Baltimore and distributed in 1919. It represents a distinct improvement over its parent variety, although the casual observer would consider it similar.

Yeager (54), of North Dakota, has done some of the most interesting tomato breeding in this country, but his work is not generally known and appreciated outside the northern Great Plains area. Yeager has bent his efforts to the development of a list of varieties adapted to a short, rather dry season in a region of wide extremes of temperature and frequent desiccating winds. These conditions are decidedly unfavorable for tomatoes in general. It is only in the last 12 years that farmers and gardeners of the northern Great Plains have had varieties that could be grown there with any satisfaction, but now they have several. Even though these varieties from the North Dakota station are adapted to the area in question and are far better there than anything heretofore available, they are of little interest elsewhere. The very characters that enable them to succeed in North Dakota appear valueless, for example, in Virginia. That, however, is no discredit to the varieties or the introducer. They serve the purpose for which they were bred, and that is enough.

The seven varieties introduced by Yeager up to this time are all early and bear their moderate crops on comparatively small plants in a short time. This is necessary in order to meet the requirements of the region. All were developed by hybridization, one of them involving an interspecies cross. Red River (Earliana  $\times$  Sunrise), introduced in 1925, and Bison (Red River  $\times$  Cooper Special), introduced in 1929, are the best known and most important thus far. The latter has shown an appreciable resistance to heat. Two yellow varieties, Fargo Yellow Pear (Bison  $\times$  Yellow Pear) and Golden Bison (Bison  $\times$  Golden Queen), introduced in 1932, meet the requirements of those gardeners who desire yellow-fruited sorts. Farthest North is of particular interest because of its parentage (Bison  $\times$  Red Currant) and its extreme earliness. It was introduced in 1934, so it may be rather too new to tell how important it is going to be. The other two of Yeager's introductions are Early Jumbo (June Pink  $\times$  Globe), distributed in 1929, and Pink Heart (Bison  $\times$  Ohio Red), distributed in 1932.

The Santa Clara (4) tomato, which is now the principal variety grown for canning in California, is the result of work by several agencies and men. It traces back to a single plant selection made in 1923 by a representative of the Cannery League, in a field of a variety called Trophy or Canner. This was not the old original Trophy previously mentioned, nor even the variety generally cataloged under that name by seedsmen. It was a large, irregular, rough-fruited sort that was wasteful and difficult to prepare for canning on account of corrugations

and catfaces, and was grown only for canning in that section. The Cannery League, the Ferry-Morse Seed Co., the California Packing Corporation, and the California Agricultural Experiment Station all contributed to the further selection and final development of this huge, moderately smooth-fruited variety that entered into commercial production about 1926. It has a very large heavy-yielding plant that produces the largest fruits of any of the extensively grown commercial sorts, but anyone who tries to grow it east of the Rocky Mountains will be disappointed in it. It is excellent in parts of California but almost a failure in other parts of the country.

In 1928 the California station released a selection from Santa Clara developed through careful inbreeding and called California 55. It was produced for its smoother fruits, high yield, and more intense red color.

The Illinois, Massachusetts, and Michigan stations have placed emphasis on greenhouse sorts because of the magnitude of the forcing industry in their States. In 1930 Illinois introduced Lloyd Forcing and Blair Forcing, both derived from Louisiana Pink  $\times$  Grand Rapids. Both varieties are wilt resistant. In 1931 Massachusetts introduced Waltham Forcing, a selection from an unknown sort for adaptation to adverse northern greenhouse conditions.

The New Jersey station distributed the Rutgers variety in 1934. It is a cross of Marglobe  $\times$  J. T. D. and has been reported especially valuable on the light sandy soils of New Jersey. The Illinois station has just released sorts that will set fruit and not grow out of bounds on the high-nitrogen prairie soils of Illinois. The Washington (State) station introduced in 1930 Seedling 36 and Seedling 50, results of crossing Bonny Best  $\times$  Best of All to obtain higher productivity under Washington conditions. They were intended to be adapted to a specific environment, hence it is not surprising that they have remained of rather local interest.

Within the last year or two many stations have released several additional strains and varieties that may or may not make important places for themselves. Small plot tests, even though numerous and fairly widespread, often fail—in fact usually fail—to reveal the true commercial possibilities of a new line and to indicate the reactions of the tomato-growing industry and the consuming public. Only time and general commercial trial can determine these things. The newer introductions, as reported by their originators, are listed in table 4 of the appendix to the vegetable articles, along with those discussed in this brief survey.

Gratifying progress has been made in the selection of verticillium and fusarium wilt resistant strains of tomato in California by Michael Shapovalov, of the Department, and B. A. Rudolph, of the California station, working cooperatively.

## PEPPERS

### HISTORY

THE hot and the sweet peppers grown in the United States belong to a quite different group of plants from the black or white pepper of commerce. The peppers that we grow in this country are *Capsicum*

*annuum* L., a New World species native to the Tropics. There are no ancient eastern names for the species, and the first record of it (1493) indicates that Columbus took the first specimens to Europe on returning from his first voyage to the West Indies. Peppers or chilis are known to have been one of the principal foods of the native inhabitants of tropical America. The pepper had already reached a fairly modern state of improvement at the time of its discovery by Europeans, as evidenced by the wide diversity of the several distinct sorts described in the early records. All the types current today were known to be used by the natives of Central America in the seventeenth century (18). It would thus seem that the prehistory of the pepper might closely parallel that of the tomato.

There seems to have been no such aversion in Europe and colonial America to the use of peppers as there was to tomatoes. Peppers were apparently adopted immediately, and their use quickly became almost worldwide. Certain types became established so promptly in India, for example, that some of the early botanists believed them native to the East. However, the name "chili", which is still used in India, strongly indicates importation from South America.

Although they were quickly adopted and have been generally used beyond their native land for over 400 years, the properties of most varieties of peppers do not make them a product to be eaten in large quantities as a staple vegetable by most users. Generally peppers, even the sweet or nonpungent varieties, form a small proportion of salads or mixed vegetable dishes. Some nationalities, however, use them more or less "straight", the Mexicans in particular consuming almost incredible quantities of them. And those who are familiar with Mexican cookery know how generously the fiery varieties are used.

#### IMPROVEMENT IN THE UNITED STATES

Since the pepper is not a major crop, it has received far less attention than its relation the tomato. Even though a few enthusiasts have effected some excellent improvements, the importance of the crop itself has not been great enough to attract much attention to more than a few of the advances made. As a result, the records concerning early improvement are very sketchy and incomplete. Unfortunately, no such dependable varietal history can be written for this crop as for the tomato.

In 1901 American seedsmen listed between 125 and 150 varietal names of peppers in their catalogs. Of this number only 18 to 20 probably denoted really distinct varieties, the others being merely synonyms or cases of misnaming. The history of those varieties, with few exceptions, is indeed obscure. It is noteworthy, however, that after 35 years these distinct sorts are all still available commercially with one or two possible exceptions. Furthermore, there have been few very distinct or very marked improvements in type. Many new names have appeared for old forms, and the old stocks have been improved in uniformity and conformity to type. The principal other improvements made have been in securing somewhat thicker flesh and increased earliness. These improvements have been effected almost entirely by private agencies.

The list of practically all really distinct sorts noted by Tracy (46, 47) follows:

## Pungent varieties—

Bird's Eye  
Cayenne  
Celestial  
Cherry  
Large Red Chili (or Mexican)  
Red Cluster  
Small Chili (Red Chili)  
Tabasco  
Yellow Cayenne  
Yellow Cherry

## Mild varieties—

Bellior Bull Nose  
Black Nubian  
Chinese Giant  
Golden Dawn  
Golden Giant  
Monstrous (or Grossum)  
Ruby King  
Squash or Tomato  
Sweet Mountain

Until recently most of the hot varieties were the same as when they were first found by Europeans over 400 years ago. One type, however, has been a subject for improvement since about 1900. The large, long, hot type variously known as a Cayenne or Mexican type, or just as plain Chili, is a very important vegetable in the Southwest. This should not be confused with either the very hot Cayenne variety or the very hot small Chili pepper that is used in making pepper sauce. It is a large elongate sort that is eaten green or ripe and used fresh, canned, or dried.

In 1903 Musser (14) introduced Anaheim Chili, named for the town of Anaheim, Calif., an important center of production and drying of this type of pepper. It was developed by mass selection from the Mexican Chili for longer, thicker-fleshed pods. It is still an important variety.

About 1917 Garcia (16), of the New Mexico Agricultural Experiment Station, introduced Chili No. 9, also a selection from the native Mexican type. He selected specifically for larger size, thicker flesh, a sloping shoulder to facilitate peeling, productivity, and general adaptability to canning under New Mexico conditions. Incidentally, he obtained an intermediate resistance to fusarium wilt. The strain has replaced most of the older ones grown in the warmer parts of New Mexico.

Recently, by pure-line selection, Miller, of the Louisiana station, has developed a number of highly uniform, intensely colored, productive strains of very hot peppers of the Tabasco and Cayenne types. The production of Tabasco peppers for making Tabasco pepper sauces is an important industry in Louisiana. In 1935 Miller distributed Tabasco 10-1 and Tabasco 10-2. These were developed from the locally grown strains of the variety. Sport was distributed in 1936. It was developed by crossing the local Sport  $\times$  Honka, an intensely red Japanese variety, then backcrossing to Honka in an effort to further intensify color. A fourth production of Miller's is Selection C-28-11, derived by inbreeding from a locally grown strain, Baton Rouge Cayenne. He selected for superior earliness, greater pungency, yield, and resistance to cercospora leaf spot.

Although the sweet varieties are much more important commercially than the hot varieties, less attention has been given to them by public research agencies in the United States. This is doubtless

because of the keen interest private agencies have shown in the sweet peppers and the very satisfactory contributions they have made.

Two sweet varieties of pepper have been introduced by experiment stations, but so recently that it is impossible now to indicate their probable importance. The Waltham Field Station of the Massachusetts Agricultural Experiment Station introduced Waltham Beauty in 1935. It was selected from an unidentified variety. The Connecticut station introduced Windsor-A in 1936, developed from a hybrid of California Wonder  $\times$  Bountiful. Both of these new introductions are early, show improved wall thickness, and are adapted to New England conditions.

Practically all of the large-fruited, mild-fleshed varieties were derived by selection or the finding of valuable segregates of natural crosses. The pepper is cross-fertilized to a considerable extent, so that under field conditions natural crosses between varieties may occur frequently. The parent varieties of most of the commercial varieties that have been prominent for the past 50 years are unknown and many of them are relatively old.

As mentioned above, the hot varieties, except for very recent improvements that hardly involve major varietal characters, have been known for 250 to 300 years and even longer. Among the sweet varieties the names of Bell or Bull Nose, Oxheart, and Squash have been current for over 150 years. Most of our present sweet varieties have come from these types. The types were first described about 400 years ago.

Just as the period from 1875 to 1900 was very productive of new introductions and selections of tomato, so it was with peppers. Although many new names and some improved stocks appeared, few really marked advances can be recorded. Many of the supposedly new introductions during that period represented varieties that could be recognized by detailed descriptions in the literature over 200 years old. We may be safe in assuming that nearly all varieties known about 1850 were very old and that about half the "new" varieties introduced between 1875 and 1900 had been known for 100 to 200 years. Table 1 shows only too well the fragmentary nature of our present knowledge of the origin of some of the better known varieties.

There are a few varieties that command special interest. Chinese Giant and Ruby King are doubtless selections out of the old Bell or Bull Nose, and Chinese Giant represents no very great deviation from its supposed parent variety. It is rather late, tends often to be rough, and is only a moderate to shy producer. Ruby King, introduced by Burpee, was a real improvement over the old type, having more attractive, uniform shape, higher productivity, and better quality. The chief claim of Chinese Giant to fame was its size. Ruby Giant and World Beater are two varieties of some importance that were developed from crosses of Chinese Giant and Ruby King. Royal King was selected from Ruby King, and Magnum Dulce, popular for many years, was selected from Chinese Giant. Although the records are incomplete, it appears almost certain that several of the more recent introductions also have been selected from one or the other of these two varieties or from crosses in which one or both were involved. Ruby King is still one of the half dozen most important

sweet varieties and is perhaps more widely grown than any other single variety. California Wonder is considered the most important improvement in many years, on account of its large size, attractive form, uniformity, and very thick, firm flesh. It is rather late, however, and not well adapted to the northern third of the United States. Harris Early Giant, introduced by the Joseph Harris Seed Co., is very popular in the more northerly areas where California Wonder is too late.

TABLE 1.—*Origin of some of the more important pepper varieties of the United States*

Name	Early reference to variety	Varietal history in United States	
		First described or advertised	Origin
Anaheim Chili.....		1903	Selected from Mexican Chili by H. L. Musser.
Bell (or Bull Nose).....	1774	( <sup>1</sup> )	Precolonial; New World.
Black Nubian.....	1753	1991	European variety.
California Wonder.....		1828 <sup>2</sup>	Selection by a California grower.
Cardinal.....		1887	
Cayenne.....	1542	( <sup>1</sup> )	Supposedly French Guiana.
Celestial.....	1731	1887	Chinese variety.
Cherry.....	1586	( <sup>1</sup> )	Precolonial; New World.
Chilli (or Chili).....	1588	( <sup>1</sup> )	Do.
Chinese Giant.....		1900 <sup>2</sup>	Selection from Bell (?).
Elephant's Trunk.....		1892	Selection from Cayenne (?).
Etna.....	1640	1890	First advertised by W. Atlee Burpee & Co.
Golden Dawn.....		1882	
Golden Neapolitan.....		1906	Chance seedling in Neapolitan.
Golden Upright.....		1887	Unknown.
Harris Earliest.....		1920	Introduced by Joseph Harris Seed Co.
Kaleidoscope.....	1632	1890	Precolonial; New World.
Long Red.....	1813	( <sup>1</sup> )	Do.
Long Yellow Cayenne.....	1832	( <sup>1</sup> )	Do.
Magnum Dulce.....		1904	Selected from Chinese Giant.
Monstrous.....		1867	Selected from Bell (?).
Neapolitan.....		1903	Italian variety.
Nepal Chili.....	1809	1895	
New Mexico Chili No. 9.....		1917	Selected from Mexican Chili by F. Garcia.
Oxheart.....		1844	
Perfection.....		1912	Selected from Spanish "pimiento" by S. D. Riegel.
Royal King.....		1918 <sup>2</sup>	Selected from Ruby King by George Riegel.
Ruby Giant.....		1906	Ruby King × Chinese Giant.
Ruby King.....		1884	First listed by W. Atlee Burpee & Co.
Squash (or Tomato).....	1686	( <sup>1</sup> )	Precolonial; New World.
Sunnybrook.....		1922	Selected from Squash. Introduced by W. Atlee Burpee & Co.
Sweet Mountain.....		1849	Selected from Bell (?).
Tabasco.....	1888	( <sup>1</sup> )	Introduced from Mexico.
Waltham Beauty.....		1935	Selection.
World Beater.....		1919	Chinese Giant × Ruby King.

<sup>1</sup> Unknown; very old.<sup>2</sup> Approximate date.

The sweet peppers of the Squash or Tomato type are very popular for home garden and local market use, but are relatively unimportant in the heavy commercial shipments. Sunnybrook, introduced by Burpee, is the best known and most important of these. A tempest raged a few years ago in the horticultural press over claims that certain varieties of this group represented hybrids between pepper and tomato. The new names involved in the controversy implied hybrid origin, and the varieties were advertised and sold with the claim that they were new hybrids. However, numerous botanists, horticulturists, and growers who know peppers and tomatoes have never been able to detect any trace of tomato characteristics in either the plant or the fruit. The tomato shape proves nothing, for that



has been known in peppers for about 400 years. Furthermore, tomato and pepper belong to such distantly related genera that crossing the two is believed to be impossible. There is, at least, no convincingly documented case of such a hybrid known, despite the fact that skillful workers have often tried to cross them.

Another interesting varietal development is that of the Perfection pimiento pepper, selected to meet a specific requirement by S. D. Riegel, of Georgia. The introducer of this variety was engaged in the canning of peppers and required a very mild, very thick-fleshed sort having specific qualities of flavor and adaptability to canning. Since no such variety was grown in the United States at that time, he obtained seed of a Spanish pimiento from Spain. The variety name was not stated, but it was probably Sweet Genua or a closely related form. From this Spanish stock a single plant was selected having the desired characters and apparent adaptability to conditions in the southern United States. The variety Perfection was developed by selection from the progeny of this plant and first introduced to the trade about 1912.

## EGGPLANT

### HISTORY

THE eggplant, *Solanum melongena* L., is believed to be native to the Tropics of the Old World. It was referred to in Chinese writings of some 1,500 years ago, and by various early writers in the sixth, ninth, twelfth, and thirteenth centuries (18). It appears to have been unknown in Europe in ancient times and is therefore believed to be Asiatic in origin. Vavilov (48) has concluded through his botanical-geographic studies that there were two centers of origin, the first in subtropical or tropical India, the second in China.

In the sixteenth century various writers described eggplants of the several colors known today—purple, yellow, white, ash-colored, green, and brownish. The oblong or elongated, pear-shaped, and round forms were also known in that early day. At present there is almost no interest in any but the purple-fruited sorts in the United States, but occasionally other colors are grown for ornament. There is good evidence that no new or distinct types have been developed within historic time, although of course numerous variations or varieties have been found and propagated within each type. It is probable that considerable increase in size has resulted from comparatively modern efforts, because the varieties described early in the seventeenth century seem to have been rather small. A hundred years later descriptions are found indicating fruit sizes that are comparable with our present sorts.

Vilmorin-Andrieux & Cie., Paris (49), in 1856 described 7 varieties, including Long Purple, Round Purple, Chinese Long White, Large Purple, and Guadaloupe Striped. Burr (5), in this country, in 1865 listed these same varieties as of interest here, and in addition described New York Improved. New York Improved and Long Purple are still among the half-dozen varieties of commercial importance in the United States today.

The eggplant does not have any great appeal to the majority of consumers in this country, so it remains a minor crop—and probably will

so remain for a long time. This general lack of interest is reflected in the small attention it has received here from plant breeders and investigators. There are few varieties grown in the United States, and little is being done to produce new ones. In the Orient, however, the situation is quite different. The eggplant is one of the most important vegetables in China, Japan, and India, holding in those countries a position more nearly comparable with that of the tomato in North America. Because of its extensive use and popularity in the Orient, numerous varieties have been developed and it has been the object of perhaps more genetic and cytological study than in Europe or North America. Numerous oriental varieties have been introduced for trial by American growers and seedsmen but have never attracted interest. Some of them are quite productive, but generally they are of small-fruited types or of colors that do not appeal to us.

### BREEDING AND IMPROVEMENT

All our important commercial varieties are the result of work by private gardeners and seedsmen. Most of them were doubtless obtained merely by selection from the old long-established types and represent minor improvements except in fruit size and uniformity. Unfortunately we are unable to determine with certainty the time, manner, and place of origin of our present varieties.

The white, striped, and scarlet-fruited sorts are all very old and are of interest only as novelties or ornaments, so they will not be discussed here.

Of the purple-fruited sorts, Round Purple and Long Purple doubtless were imported from Europe a century or more ago. Vilmorin-Andrieux & Cie. (49) lists Large Purple as of American origin, introduced in 1854. The parentage is unknown.

Burr (5) lists New York Improved, indicating that it was derived from Large Round. It was described as having spiny leaves. It appears that the variety was developed by selection about 1850 by Brill, a gardener and seed grower of Long Island, N. Y., and named by him. The modern strains of New York Improved are spineless. Spineless strains have been available since about 1900.

Black Pekin was a popular variety for many years but is now rarely listed. It was introduced from China about 1870.

Black Beauty appeared about 1900. It is said to have been originated by Ashcraft, a gardener and seed grower of Swedesboro, N. J. There is little question that Black Beauty has been the most popular eggplant variety grown in the United States. The intensely dark-purple, or purplish-black, fruits of medium-large size are very attractive and are largely responsible for its outstanding prominence.

The old Long Purple variety has been the subject of selection for earliness, particularly in the Northern States. Early Long Purple, or simply Long Purple, is the earliest variety commonly grown, but is grown extensively only where earliness is essential.

The most important development since Black Beauty is the Florida High Bush. It was introduced about 1905 by a Florida grower who selected it for its tall upright growth and habit of bearing its fruits well up off the ground. This character is often of considerable im-

portance as an aid in avoiding losses from fruit rots or other damage resulting from contact with the soil.

The agricultural experiment stations of New Hampshire, Rhode Island, and Wisconsin are all working for increased earliness in eggplant to permit its being grown profitably farther north. The Central Experimental Farm of Canada, at Ottawa, has introduced Blackie, a selection smaller and earlier than Black Beauty that is also more productive in the North.

Kakizaki (25), in Japan, demonstrated the commercial feasibility of artificially produced hybrid eggplant from inbreds known to be superior for the purpose. In 1931 he introduced Black Bountiful, a first-generation hybrid which has been offered for sale in the United States by Japanese seedsmen. It is distinctly smaller than our well-established sorts and so has not become popular here. However, it is early and very productive.

## STUDIES OF INHERITANCE AND CYTOLOGY IN SOLANACEOUS FRUITS <sup>5</sup>

### TOMATO

THE first investigators (17, 41) of the mode of inheritance of specific characters in the tomato quite naturally and logically examined certain of the most obvious features of plant and fruit, such as cotyledon size and shape, leaflet size and shape, leaflet surface character, plant stature, growth habit, fruit color, fruit shape, and internal structure of fruits. Such studies have been made over the last 30 years, but the most conclusive results have been reported in the last 15 years. J. W. MacArthur, at the University of Toronto, and E. W. Lindstrom, at the Iowa Agricultural Experiment Station, are the most active in studying inheritance in "normal" individuals, while J. W. Lesley and M. M. Lesley in California, F. W. Sansome in England, besides Lindstrom, are engaged with cytological studies, induced mutations, polyploidy, and the occurrence of aberrant forms.

A large number of workers have contributed to the present knowledge of inheritance of specific characters in the tomato, but it is not necessary to cite here all the literature of all workers. Table 2 presents a summary of the characters studied to date, with data concerning dominance and indications as to whether the contrasted characters are due to differences in one or more factors. Most of those listed represent single factor differences.

Unfortunately, the characters that we most desire to incorporate into our new varieties to meet new needs cannot be listed in the table at this time. These are resistance to specific diseases, such as fusarium wilt, verticillium wilt, nailhead, leaf mold, septoria, mosaic, streak, and curly top. Although there are many varieties showing a fairly high resistance to fusarium, a few resistant to nailhead, and resistance to leaf mold, nothing certain is known about the number of factors involved in resistance to any of these diseases, and there are only general unconfirmed indications of the dominance or recessiveness of resistance.

<sup>5</sup>This section is written primarily for students or others professionally interested in breeding or genetics.

TABLE 2.—*Inheritance in the tomato*

Characters	Genes	Behavior in F <sub>1</sub>	Segregation in F <sub>2</sub>	Authority	Tetraploid segregation (after Sansome, 44)
Flesh color:					
Red <i>v.</i> yellow .....	<i>R-r</i>	Red.....	3 red to 1 yellow.....	(17, 29, 34, 37, 41)	Between 22:1 and 35:1
Red <i>v.</i> tangerine orange.	<i>T-t</i>	...do.....	3 red to 1 tangerine orange.	(34, 37).....	
Skin:					
Yellow <i>v.</i> colorless.....	<i>Y-y</i>	Yellow.....	3 yellow to 1 colorless.....	(17, 29, 34, 37, 41)	Approximately 35:1. Approximately 22:1.
Dark-green base <i>v.</i> uniform green fruit.	<i>U-u</i>	Dark-green base.	3 dark green to 1 uniform.	(37).....	
Smooth <i>v.</i> pubescent.....	<i>P-p</i>	Smooth.....	3 smooth to 1 pubescent.	(17, 29, 34, 37).....	
Shape of fruit:					
Globe <i>v.</i> pear.....		Globe.....	Gradations. Tend toward 3:1.	(34, 37).....	
Short <i>v.</i> elongated.....	<i>O-o</i>	Short.....	3 short to 1 elongated.....	(29, 34, 37).....	
Normal <i>v.</i> fasciated.....	<i>F-f</i>	Normal.....	3 normal to 1 fasciated.....	(34, 37).....	
Normal <i>v.</i> nipple-tipped.....	<i>N-n</i>	...do.....	3 normal to 1 nipple-tipped.	(34, 37).....	
Locules in fruit:					
2 locules <i>v.</i> many.....		2 locules.....	Approximately 3:1.....	(41).....	
Size of fruit:					
Large <i>v.</i> small.....		Intermediate	All gradations.....	(29, 30, 36, 37, 41)	
Plant habit:					
Tall <i>v.</i> dwarf.....	<i>D<sub>1</sub>-d<sub>1</sub></i>	Tall.....	3 tall to 1 dwarf.....	(17, 29, 37, 41).....	Approximately 22:1.
Dwarf <i>v.</i> extreme dwarf.....	<i>D<sub>2</sub>-d<sub>2</sub></i>	Dwarf.....	3 dwarf to 1 extreme dwarf.	(34, 37).....	
Tall <i>v.</i> brachytic.....	<i>B<sub>1</sub>-b<sub>1</sub></i>	Tall.....	3 tall to a brachytic.....	(34, 37).....	
Normal <i>v.</i> self-topping.....	<i>Sp-sp</i>	Normal.....	3 normal to 1 self-topping.	(34, 37).....	
Leaves:					
Green <i>v.</i> yellow color.....	<i>I-l</i>	Green.....	3 green to 1 yellow (lutescent).	(17, 34, 37, 41).....	
Normal <i>v.</i> potato leaf.....	<i>C-c</i>	Normal.....	3 normal to 1 potato leaf.	(17, 34, 37, 41).....	
Normal <i>v.</i> wiry.....	<i>W-w</i>	...do.....	3 normal to 1 wiry.....	(34, 37).....	
Normal <i>v.</i> wilted.....	<i>W<sub>1</sub>-w<sub>1</sub></i>	...do.....	3 normal to 1 wilted.....	(34, 37).....	
Normal <i>v.</i> hairless.....	<i>H-h</i>	...do.....	1 normal; 2 intermediate; 1 hairless.	(34, 37).....	
Inflorescence:					
Simple <i>v.</i> complex.....	<i>S-s</i>	Simple.....	3 simple to 1 complex.....	(34, 37).....	Approximately 22:1.
Normal <i>v.</i> leafy.....	<i>Lf-lf</i>	Normal.....	3 normal to 1 leafy.....	(34, 37).....	
Stem color:					
Purple <i>v.</i> green.....	<i>A<sub>1</sub>-a<sub>1</sub></i>	Purple.....	3 purple to 1 green.....	(34, 37).....	
Purple <i>v.</i> becoming green.....	<i>A<sub>2</sub>-a<sub>2</sub></i>	...do.....	3 purple to 1 becoming green.	(34, 37).....	
Time of maturity:					
Early <i>v.</i> late.....		Intermediate	All gradations.....	(7).....	
Pedicle:					
Jointed <i>v.</i> nonjointed.....	<i>J-j</i>	Jointed.....	3 jointed to 1 nonjointed.	(6).....	
Hereditary radium-induced mutations of Lindstrom: <sup>1</sup>					
Leaves:					
Normal <i>v.</i> rough.....	<i>R<sub>1</sub>-r<sub>1</sub></i>				
Normal <i>v.</i> yellow.....	<i>L-l</i>				
Cotyledons:					
Normal <i>v.</i> rolled.....	<i>R<sub>c</sub>-r<sub>c</sub></i>				
Sterility:					
Normal <i>v.</i> sterile.....	<i>S<sub>t</sub>-s<sub>t</sub></i>				
Seedlings:					
Normal <i>v.</i> yellow (lethal).....	<i>Y<sub>1</sub>-y<sub>1</sub></i>				
Normal <i>v.</i> virescent white.	<i>V-v</i>				

<sup>1</sup> All 6 characters monorecessives; *l* shown to be same character previously known (32).

Several difficulties have stood in the way of acquiring this much-needed information. First, strong resistance to certain of these diseases is at present unknown in any form of tomato. Wide search has yielded no appreciable resistance to mosaic, streak, or curly top. And in those cases where a degree of resistance is known, it is usually such an intermediate or partial resistance that it cannot be measured with any dependability. Until methods are developed that will permit accurate determination of the amount of resistance in a plant, under even a single set of reasonably standardized experimental conditions, progress will necessarily be slow. It must be possible to repeat tests with given stocks and get results that will consistently agree if we are to know much about resistance.

Another difficulty is space requirement and cost of conducting such tests with the tomato. Thousands of small-grain plants or peas can be tested on a few square rods of land or a few benches in the greenhouse; but in the field, 15 to 20 square feet is needed for each tomato plant, and 3 to 4 square feet of precious space in the greenhouse. The worker with small plants can test thousands or hundreds of lines where the tomato investigator can handle only hundreds or dozens.

There also has been too much pressure for quick practical results, and many workers have felt it necessary to hurry without being able to make the desirable and often essential preparatory surveys and studies. Now a number of research agencies are backing up for a new start, but they are first carefully preparing to ferret out essential basic information before launching further into practical application of research. It is hardly possible to apply what isn't known.

In his quest for leaf-mold resistance, Alexander (1), at the Ohio station, has isolated apparently homozygous resistant lines from segregating progenies of a cross between an off-type resistant plant and the variety Marhio. The off-type plant bore very small fruits on simple inflorescences and appeared to be from a chance cross with the Red Currant variety. Von Sengbush and Loschakowa-Hasenbusch (45) have reported that *Solanum racemigerum* Lange (known in the United States as *Lycopersicon pimpinellifolium* Mill.) is completely resistant to leaf mold and that resistance in this species is due to a single dominant factor. They have also reported a recessive form of resistance in the variety Stirling Castle. Alexander's data, although admittedly meager and not taken as part of a genetic study, also indicate a recessive resistance in Stirling Castle and a dominant resistance in Satisfaction, another English greenhouse sort.

D. R. Porter, at the California station, has noted appreciable resistance in *L. pimpinellifolium* to western yellow blight, a virus disease, and is attempting through crossing and backcrossing to incorporate the resistance rapidly into acceptable commercial types. He is also studying the genetics of resistance.

Porte and Wellman, of the Bureau of Plant Industry, found one line of *Lycopersicon pimpinellifolium*, when grown in heavily artificially infected fusarium wilt soil, to be practically immune to wilt and highly resistant to a number of leaf diseases. They used a technique similar to Porter's in order to transfer higher degrees of fusarium resistance to commercial sorts than they commonly carry. By controlled pollination they have also developed a large number of inbred lines of

commercial varieties resistant and susceptible in all degrees. This was preparatory to determining the nature of such disease resistance as the lines possessed, which might be used in further breeding. It has not been possible to observe consistent percentages of resistant and susceptible individuals in repeated tests of a stock or line, or consistent degrees of injury to the plants in repeated inoculation tests. The effects of the texture, moisture, hydrogen-ion concentration, soluble salts, temperature, and fusarium content of the soil, the temperature and humidity of the air, the effect of light, age, and size of plant, and other such factors upon infection and reaction of the plant to the parasite are almost if not entirely unknown. These must be learned and test conditions properly standardized before dependable comparisons of resistance can be made. Special studies are, therefore, in progress in efforts to perfect a technique for dealing with the incomplete type of fusarium resistance, the only type definitely reported to date.

C. M. Tucker, at the Missouri station, has recently reported to the writer that among many seed lots of *Lycopersicon pimpinellifolium* tested, one appears to possess complete dominant resistance to fusarium wilt. Other lots either were 100-percent susceptible or showed the intermediate resistance that is typical of resistant commercial varieties. At this writing his studies have not proceeded far enough to determine more.

A number of other investigators are busy with disease resistance and with selection for improved adaptation to specific requirements, but reports are not now available as a basis for discussing their work. (See list of projects and workers in the Appendix.)

Wellington (51) reported yields of  $F_1$  intervarietal hybrid tomatoes about 21 percent higher than the yields of the more productive parent, 45 percent higher than the mean of the two parents, and 71 percent higher than the lower yielding parent.

### Linkage in the Tomato

Thus far, the chromosome map of the tomato hardly has its outlines well drawn. MacArthur (34, 35, 36, 37) and Lindstrom (29, 30, 33) have made the major contributions to knowledge of this problem. Of some 20 genes that are known, the positions of 16 have been located on 10 of the 12 pairs of chromosomes. Six of the groups now contain two or more known genes.

The chromosome map showing the linkage groups and the probable order of the genes within the groups may be represented roughly as follows:

Chromosome	Genes	Chromosome	Genes
I	$D_1-P-O-S$ (and genes for earliness ?).	VI	$L$ (and genes for earliness and size ?).
II	$R$ (?).	VII	$U-H-T$ .
III	$B_r-Y$ .	VIII	$A_2$ (?).
IV	$C-S_p$ .	IX	$D_2$ (?).
V	$F-A_1-L_f-J$ .	X	$W_r-N$ .

The second, sixth, eighth, and ninth chromosomes each bear but one known factor.

Currence (7) has recently pointed out a relation between genes of the *D<sub>1</sub>POS* region of the first chromosome and genes affecting earliness. The actual nature of the factors involved has not been determined, but *D* and *DP* lines were, on the average, 9 and 14 days earlier respectively than corresponding *d* and *dp* progenies.

MacArthur (36) has also recently added evidence of a possible linkage of genes for earliness and size—if there are such—with certain qualitative factors. He showed that *l*, a recessive gene for yellow-green foliage, retards maturity about 2 weeks and reduces fruit size 30 percent. The author recognized that the existence of size and earliness genes linked with *l* was not demonstrated, for the effect might possibly be due directly to *l* or other genes. It is logical to suppose that *l* would have a marked direct effect on plant and fruit development.

It is unfortunate that we do not yet have accurate information regarding inheritance of disease resistance and possible linkages with qualitative genes. Some observations might lead us to suppose that at least certain types of resistance are linked closely with specific characters.

### *Cytology of the Tomato*

Thus far very little if any attention has been given to the cytology of hybrids of *Lycopersicon esculentum* Mill. and related species. The large number of small chromosomes make cytological study quite difficult. In the intensive drive for disease resistance, however, it seems sure that wider and wider crosses will be attempted, with the failures, sterilities, and various aberrations that accompany such efforts. Workers will then find it necessary to study both the normal and the abnormal material cytologically more than has been done in the past.

Most of the cytological work done on the tomato has been in the study of triploids, trisomics, and both natural and artificially induced tetraploids. All three of these chromosomal aberrations occur rather frequently in cultivated fields and may become evident through the departure of the plant from the typical vegetative form and fruitfulness of the variety in which the aberrations appear. A number of these have been described in detail by Lesley (26, 27), Lindstrom (31), and others. In general the plants are characterized by a sturdier, stockier appearance; thicker, more rugose leaves; and little or no fruit. They generally produce a large proportion of abortive pollen and may be unfruitful for that reason if not for others.

The normal *n* number of chromosomes in the tomato is 12, and the *2n* or somatic number is 24. Aberrant plants have been found with 25, 26, 27 (aneuploids), 36 (triploids), and 48 (tetraploids) somatic chromosomes, and also some with fragments of additional chromosomes. Lesley (27) has obtained 12 different simple trisomics, each with a different supernumerary chromosome, by crossing a triploid (*2n*=36) plant with a normal diploid (*2n*=24). He has identified these as Triplo-A, Triplo-B, Triplo-C, etc., depending on which one of the 12 chromosomes occurred as a supernumerary. These identifications of extra chromosomes and the determinations of trisomic ratios in the progenies of hybrid trisomics have afforded additional confirmation of the connection between genes and chromosomes and may add

to knowledge of linkage relations. An understanding of what is happening to the chromosomes of these aberrant plants helps to make it clear why they will not breed true and why it is so difficult, if not impossible, to make practical use of certain desirable characters that some of them have.

Several workers—Winkler (52), Jørgensen (23), Sansome (44), and others—in addition to those already named have induced the formation of tetraploids by cutting off stems of plants. Callus tissue rapidly forms under proper conditions, and in this tissue cells are occasionally formed with 48 instead of 24 chromosomes. Some of these cells may develop into shoots and continue growth in a more or less normal manner. Since these tetraploids are usually nearly sterile or quite so, and since they do not breed true, they are usually propagated vegetatively for experimental purposes. Thus far there is no proved case of a commercially valuable tetraploid.

Lindstrom (31) has reported a highly fertile tetraploid of *Lycopersicon pimpinellifolium* obtained from callus tissue, but it is apparently the only such case noted. Some are inclined to believe that the parent plant was not homozygous but that *L. esculentum* was involved. The tetraploid was cross-sterile with the parent type.

A variation with less than the normal number of chromosomes has also been observed. Lindstrom has described a haploid tomato (12 somatic chromosomes as well as 12 in the germ cells). It was found in the  $F_2$  of a varietal cross of completely fertile varieties. The haploid was smaller than normal and almost completely sterile. Its pollen was apparently impotent and few seeds were borne when other pollen was applied to its flowers. There was no tendency to pairing of the chromosomes, but evidence of a tendency toward reduction or separation in the meiotic division. It appeared that any germ cell receiving less than 12 chromosomes aborted.

A few diploid cells were noted in roots, so the plant was carefully perpetuated by cuttings in the hope that doubling might occur in a cell destined to become a growing tip and thus give rise to an absolutely homozygous tomato. Not only diploid but tetraploid plants were finally obtained.

Lesley and Lesley (28) have obtained tomato plants bearing fragments of single chromosomes by crossing a double trisomic ( $2n+1+1$  chromosomes) with a normal plant. Certain of the progenies of this cross variously contained  $2n+1$ ,  $2n+1+a$  fragment or  $2n+a$  fragment. These fragments or incomplete supernumerary chromosomes represent a partial trisomic condition. Such plants resemble certain trisomics. It has been found that fragmentation occurs in those unpaired chromosomes that lag behind in the course of meiosis.

The results of chromosome injury or of "knocking out" factors from chromosomes by irradiation may well be considered at this point. Lindstrom (32) irradiated various portions of tomato plants with radium-bearing needles. Irradiation of growing tips induced the most variations in the progeny of the treated plants. The irradiated parent plants showed no sudden variation except what could be accounted for as a result of direct injury by the radium in cases of over-dosage. The progeny of these plants, however, showed much sterility,



pollen abortion, and malformation, supposedly caused by chromosome damage.

From these progenies Lindstrom isolated six variations that bred true and were shown to be due in each case to a single recessive factor. Five of these never before had been observed in tomato, while *l* for yellow foliage was shown to be the same factor that had been known for many years (table 1).

MacArthur (38) accomplished somewhat similar results by irradiating seeds with X-rays. All plants and fruits from these seeds were normal, but their progeny showed 12.4 percent of mutants of diverse forms—all of them economically worthless. There were many lethals and semilethals among them, only about a dozen being capable of perpetuation in the homozygous condition. Most of the variations appeared as chlorophyll and leaf abnormalities, and the plants were very slow-growing. Most of the new characters susceptible of genetic study, as in Lindstrom's radium-induced variations, behaved as single recessive factors.

### PEPPER

The principal contributions to the knowledge of inheritance in the pepper have been made by Halsted (17), Webber (50), and Dale (8, 9, 10) in this country, Ikeno (20, 21) in Japan, Atkins and Sherrard (2) in England, and Deshpande (11) in India. These workers are in general agreement on the inheritance of a number of characters but disagree on others. In cases of disagreement it appears that the more recent workers are probably more nearly correct because they have generally used larger progenies and have studied the results in  $F_3$  and backcross generations as well as in the  $F_1$  and  $F_2$  generations. In some of the earlier work the importance of environment in its effect on expression of specific characters was not fully appreciated and difficulties were encountered. In table 3 are presented data on the inheritance of 16 characters in pepper. Conflicting data are not presented, but only those believed to be most dependable as indicated by the respective experimental procedures.

All investigators of foliage and flower color agree on the dominance of purple *A* over nonpurple *a* and on the close linkage or identity of factors responsible for foliage and flower color. Deshpande (11), however, only recently pointed out the effect of a second factor for purple foliage, an intensifier, *B*, which is without effect when *A* is absent. Numerous workers agree that red color of the ripe fruit is dominant over yellow and that green color of the immature fruit is dominant over yellow. Each is due to a single factor. Again Deshpande (11) contributed new information when he showed the effect of *A* upon fruit color. Plants with purplish-red fruit crossed with pure yellow gave four color types in a typical dihybrid 9:3:3:1 ratio in the  $F_2$ , namely, purplish red, pure red, yellow overcast with purple, and pure yellow. He also pointed out a close association between fruit color and seed color. Red fruits bear reddish-yellow seeds, while yellow fruits bear light or pale yellowish seeds.

Dale (8) plotted size distribution curves of pod lengths of  $F_1$  and  $F_2$  progenies of Coral Gem  $\times$  Anaheim Chili (short  $\times$  long pod) and certain backcrosses. The curves were skewed when plotted against class intervals of equal arithmetical magnitude, but were normal when plotted

on a logarithmic basis. It was concluded that the several undetermined factors for pod length exerted proportionate rather than additive effects, and that there was no disturbing influence of dominance.

TABLE 3.—*Inheritance in the pepper (Capsicum annum)*

Characters <sup>1</sup>	Genes	Behavior in F <sub>1</sub>	Segregation in F <sub>2</sub>	Investigators
Plant habit: Normal <i>v.</i> dwarf.....		Normal.....	3 normal to 1 dwarf.....	Dale (10).
Flower color: Violet <i>v.</i> white.....		Intermediate violet.....	3 violet to 1 white.....	Ikeno (20), Deshpande (11).
Foliage and stem color: <sup>2</sup> Purple <i>v.</i> nonpurple.....	<i>A-a</i>	Intermediate purple.....	3 purple to 1 nonpurple.....	Deshpande (11).
Intense <i>v.</i> normal purple.....	<i>B-b</i>	Intermediate purple (intensifier only).	Together with <i>A</i> gives 1:3:8:4, three grades purple, 1 nonpurple.	Do.
Fruit color: <sup>3</sup> Red <i>v.</i> yellow or orange.....	<i>R-r</i>	Red.....	3 red to 1 yellow or orange.	Several.
Green <i>v.</i> yellow (immature).		Green.....	3 green to 1 yellow.....	Webber (50), Deshpande (11).
Fruit shape: Blunt <i>v.</i> nonblunt apex.....	<i>D-d</i>	Intermediate.....	3 not blunt to 1 blunt.....	Deshpande (11).
Bulged <i>v.</i> nonbulged base.	<i>F-f</i>	Bulged.....	3 bulged to 1 nonbulged.....	Do.
Fruit position: Pendent <i>v.</i> erect.....	<i>P-p</i>	Mostly pendent.....	3 pendent to 1 erect.....	Deshpande (11), Kaiser (24).
Fruit calyx: <sup>4</sup> Nonclasping <i>v.</i> clasping.....	<i>E-e</i>	Nonclasping.....	3 nonclasping to 1 clasping.	Deshpande (11).
Fruit flavor: Pungent <i>v.</i> mild.....		Pungent.....	3 pungent to 1 mild.....	Webber (50).
Fruit size and shape: Large <i>v.</i> small.....		Intermediate.....	All grades.....	Several.
Elongate <i>v.</i> globose.....		do.....	Many grades; 3 factors indicated.	Deshpande (11).
Pedicle length: Short <i>v.</i> long.....		Short.....	3 short to 1 long.....	Do.
Pubescent foliage: Pubescent <i>v.</i> glabrous.....		Intermediate.....	15 pubescent to 1 glabrous.	Ikeno (20).
Inflorescence: Nonumbel <i>v.</i> umbel.....		Nonumbel.....	3 nonumbel to 1 umbel.....	Do.

<sup>1</sup> Hybrid vigor pronounced in plant vigor, height, yield, increased earliness, and fruit diameter (Deshpande (11)). Length of pedicle, petal, and fruit linked with plant color and fruit position; these in turn linked with fruit color. All these factors on 1 chromosome (Deshpande (11)).

<sup>2</sup> Purple of stems and foliage closely linked with flower color; *A* affects fruit color, giving typical dihybrid ratio 9:3:3:1 in F<sub>2</sub>.

<sup>3</sup> Seed color closely linked with flesh color.

<sup>4</sup> Nonclasping calyx closely linked with bulged base; 3 percent cross-over.

Branching habit, leaf size, and fruit size were shown by Webber (50) and others to be controlled by several factors, as evidenced by the intermediate character of the F<sub>1</sub> and the occurrence of all gradations of habit or size in the F<sub>2</sub>.

Kaiser (24) showed the hereditary position of the fruit (pendent *v.* erect) to be due to a response to geotropic stimulus rather than orientation with reference to the plant axis or branch. A single dominant factor is responsible for the pendent position.

Dale (10) studied a leaf variegation in the pepper, which he found to be inherited maternally. Ikeno (21) observed other variegated forms in which the variegation was transmitted by either male or female gamete. Selfing of these races yielded only variegated offspring. Crossing variegated with green resulted in dilution of the variegated character. Cytoplasmic transmission is thought to have

been involved in both these instances. Other workers dealing with other plants have reported many cases of apparently cytoplasmic inheritance, particularly in cases of leaf variegation.

With one exception, all reports on the chromosome number of pepper are in agreement. Kostow, according to Huskins and La-Cour (19), reported a haploid number of 6 for *Capsicum annuum*, but later workers have consistently reported 12. Huskins and La-Cour (19) studied a dozen varieties among three subspecies and found only normal figures of 12 chromosomes in the haploid and 24 in the diploid states. Dixit's (12) results agreed with these.

No such interesting observations of polyploidy have been made in pepper as in tomato. It can hardly be said that polyploidy does not occur in pepper, but a search of recent literature failed to reveal record of studies of polyploids or chromosomal aberrations in this plant. Cases will come to light as the cytologist turns more attention to it, no doubt, for the family Solanaceae is one of the most productive of these types of variation.

### EGGPLANT

As mentioned above, the eggplant has been studied very little from the cytogenetic standpoint, and most of the work done has been by other than United States investigators.

Halsted, of New Jersey (17), Nolla (39), of Puerto Rico, studying at Cornell University, and Kakizaki, in Japan (25), have studied the inheritance of color.

Halsted found two pairs of genes for fruit color. Purple skin *v.* colorless skin is due to a single dominant gene, as is also green flesh *v.* white flesh. He obtained four color types—*PG* purple (purple skin, green flesh), *Pg* pink (purple skin, white flesh), *pG* green (colorless skin, green flesh), and *pg* white (colorless skin, white flesh). He also studied a variegated fruit color that he found to be recessive.

Nolla confirmed Halsted's studies on fruit color and extended his observations to leaf and stem color, corolla color, and a striping of the anther. He found purple color in vegetative and floral parts to be either very closely linked with fruit color and with each other or controlled by the same gene. Without exception fruits with purple skins were borne on plants with violet or purple corollas and purple-tinged foliage. Green-fruit forms were borne on pure green plants with white corollas. Violet or purple corolla *v.* white was due to a single dominant factor, as was striping *v.* nonstriping of the anther. Monohybrid ratios in close conformity to the theoretical were obtained in the  $F_2$  for all these characters.

In his studies of hybrid vigor in eggplant, Kakizaki (25) determined the seed and fruit weights, stem diameters, and heights of some 30 intervarietal crosses. He also recorded the  $F_1$  behavior with reference to branching habit, leaflet size, fruit shape, color, and occurrence of calyx spines.

In the  $F_1$  generation branching, leaflet size, fruit shape, and calyx spines were intermediate between the parents. Purple skin was dominant over white.

The mean seed weight of 30 crosses was 18 percent heavier than that of the mother parents. These results were generally consistent in 3

successive years, and were compared with selfed maternal parent seeds grown in the respective years.

The  $F_1$  plants showed a mean stem diameter and height increase of 6 percent over the mean of the parents, and 36 percent increase in yield. The  $F_1$  progenies were 70 percent more productive than the lower yielding parent and 17 percent more than the higher yielding parent. The best two parents for crossing gave  $F_1$  progenies 90 percent more productive than the standard. Other Japanese workers have also noted marked hybrid vigor in eggplant. This work led to the commercial production of hybrid seed mentioned above.

It does not follow, however, that all intervarietal crosses will prove to be subsequently productive in all respects. Rao Balaji (43) has noted a high degree of partial sterility in the  $F_1$  plants of certain wide crosses of Indian varieties. The pollen was 90 to 95 percent abortive.

Yasuda (53) has induced the formation of fair-sized parthenocarpic eggplant fruits by pollinating the flowers with petunia pollen. Cytological study showed that the petunia pollen tubes never reached the micropyle of the eggplant ovule, indicating that the stimulus of pollination alone induced ovary development. Injections of an extract of petunia pollen into ovarian tissue of the eggplant produced a similar effect, but tomato pollen extract was less effective.

The haploid chromosome number of eggplant is 12, the diploid 24. A few cases of polyploidy have been observed, but thus far none has any economic value. Janaki Ammal (22) found a tetraploid in a field culture that was nearly barren. Among the progeny of this tetraploid, triploids (36 chromosomes), tetraploids (48), and aneuploids of 44 to 46 chromosomes were found. He concluded that the triploids arose from a diploid pollen grain. Selfing of one of the triploids yielded 14 seeds, which produced 13 living plants. Of these, 2 were tetraploids and 11 were near-tetraploids, the counts of which could not all be determined with certainty. All these plants with aberrant chromosome numbers were decidedly undesirable from an economic standpoint and were almost entirely sterile.

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